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Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery

Implementing Genomic Selection in CGIAR Breeding Programs Workshop Participants

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1 **Genomic prediction unifies animal and plant breeding programs as platforms**
2 **for biological discovery**

3

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14

15 **Abstract**

16 The rate of annual yield increases for major staples must more than double relative to
17 current levels in order to feed a predicted global population of 9 billion by 2050. Controlled
18 hybridization and selective breeding have been used for centuries to adapt plant and
19 animals species for human use. However, achieving higher, sustainable rates of
20 improvement in various species will require renewed genetic interventions and dramatic
21 improvement of agricultural practices. Genomic prediction of breeding values has the
22 potential to improve selection, reduce costs, and provide a platform that unifies breeding
23 approaches, biological discovery, tools and methods. Here we compare and contrast some
24 animal and plant breeding approaches to make a case for bringing the two together by the
25 application of genomic selection. We propose a strategy for the use of genomic selection as
26 a unifying approach to deliver innovative 'step changes' in the rate of genetic gain at scale.

27 **Introduction**

28 The global food price crisis of 2008 highlighted the necessity for innovation in agriculture to
29 address food insecurity in the presence of a changing climate and a growing population.
30 The world population is predicted to reach 9 billion within the next 35 years, requiring a 70-
31 100% increase in food production relative to current levels¹⁻⁴. A burgeoning world
32 population is not the only threat to global food security. Changing life styles, population
33 demographics, competition from subsidized biofuels, deterioration of natural resources,
34 climate change, and dwindling supplies of water will require considerable financial,
35 intellectual and research investment in agriculture, particularly in the developing world^{1,2,4}.
36 Breeding of livestock and crops is one of the key routes through which this increased
37 production, efficiency and sustainability can be delivered.

38 In this Perspective we outline both the opportunities and challenges for the deployment of
39 genomics in breeding programs, drawing attention to the fundamental role that
40 quantitative genetics has played as the intellectual cornerstone of plant and animal
41 breeding for the past century. Access to large scale sequence and phenotype information at
42 unprecedented scales will bring opportunities to unify breeding methods, tools, and
43 technologies across several plant and animal species, which in turn will catalyze the
44 modernization of breeding programs. Furthermore, we postulate that the adoption of these
45 new technologies and approaches at scale will enable breeding programs to be platforms
46 for both the delivery of new products and discovery biology based on genome wide
47 association studies (GWAS) and field validation of novel alleles.

48 **A brief history of plant and animal breeding**

49 Breeding of livestock and crops is as old as agriculture itself. At the heart of all breeding
50 remain such traditional pursuits as designing and analyzing performance trials to rank
51 selection candidates in order of merit, with the aim of maximizing selection gain per unit of
52 resources expended⁵. The history and development of scientific animal and plant breeding
53 can be traced back to contributions of many individuals, but there are a few outstanding

contributions, at least from our current scientific perspectives (see Figure 1). These have been extensively reviewed elsewhere and will only be discussed briefly here.

Figure 1

Despite the conceptual similarities between animal and plant breeding, their theoretical concepts and breeding methods have diverged. This is mainly because of differences in the development and application of new breeding technologies and methods⁵. While the divergence between animal and plant breeding is rather nuanced by species-specific characteristics, e.g. mode of reproduction and number of progeny per reproduction cycle, the two have developed clearly different theoretical concepts, tools and methods. For plants, although breeding can be regarded as starting with domestication, for the vast majority of the past 10,000 years it has consisted of selection only, with no enforced crossing: the sexual mechanism in plants and the need for hybridization has only been generally recognized in the last 250 years⁶. In animals, artificial selection of necessity also involved sex to create progeny and a more structured approach to breeding was adopted earlier with the use of “herd-books” to trace the pedigree of selected animals⁷.

Following the rediscovery of Mendel’s laws in the early 20th century, plant breeders started selecting and crossing superior individuals, moving on from (in some species at least) developing and maintaining cultivars by (unknowingly) harvesting selfed seed or clonal propagation. The highlights of animal breeding developments over the 20th century have centered on improving exploitation of information from relatives; through selection indices⁸, estimating breeding values as random effects⁹ and statistical methods to estimate these relationships¹⁰. Galton developed the concept of regression (essentially heritability) from which response to selection can be predicted¹¹ and Fisher developed a theory to demonstrate that the mean trait value of polygenic traits can change markedly under selection with only a small change in allele frequencies at individual loci¹².

Both plant and animal breeders deal with complex traits, but individual mutations with moderate to large effects have been exploited more widely in plant breeding than animal breeding (for example, resistance to yellow (stripe) rust in wheat¹³ and the dwarfing genes in wheat and rice). Most traits in animal breeding, in common with some important plant traits like yield, are typically polygenic. Additionally, plant breeders can usually generate genetically identical individuals or reproducible cultivars and test them in well-designed trials while animal breeders have to rely on unbalanced phenotypic data (usually) from individual animals in different production units. As a result, animal breeders were naturally forced to use complex statistical methods to estimate breeding value whereas plant breeders used well-designed trials to measure phenotype to inform their selection.

Animal breeders often have to use information from relatives of selection candidates because they have to select for traits that cannot be measured on the candidates themselves (e.g. milk yield in bulls), that have low heritability, or that are measured late in the breeding process. Plant breeders do not generally have the problem of ‘sex-limited’ traits and can experimentally increase selection accuracy by growing more plants of the same cultivar. As a result, the merit of a cultivar in a plant breeding program can often be measured to any level of precision that the breeder desires. Reproductive rates and expense make this approach harder for animal breeders to follow. A comparison of typical plant (an inbreeding cereal) and animal breeding approaches is shown in Figure 2.

Figure 2

Modern quantitative methods, including computer simulation, are pivotal to, and underpin, a host of new technologies and approaches that are of critical importance for the future of plant and animal breeding¹⁴. Many plant breeders view selection as a process of accumulating favorable genes within a single line and use a Mendelian approach to identify and incorporate favorable major genes. In contrast, animal breeders have viewed response to selection as a slow increase in the frequency of favorable alleles in a population, predictable from the ‘breeders’ equation’¹⁵. Animal breeding has therefore deployed a more classical biometrical approach combining phenotype, pedigree and genotype information from records of individuals to build estimates of breeding value to inform selection decisions. Similar approaches are also deployed in outbreeding crops such as maize and forages (e.g. in hybrid breeding¹⁶), though quantitative genetics in plant and animal breeding have developed largely in parallel with difference focuses: for animals on the statistical partition of phenotypic variation in a population into genetic and environmental components, and for plants on the outcome of crosses between two inbred lines¹⁷ with emphasis on identifying “transgressive segregants” with merit exceeding that of the best parent. Furthermore, since the 1980’s plant breeders have utilized various biotechnologies such as transgenics to a much greater degree and perhaps consequently have made much more explicit use of physiology than animal breeders. On the other hand, animal breeders have perhaps more systematically incorporated economics in the definition of their breeding goals than plant breeders. All of this has meant that the fields of plant and animal breeding have diverged somewhat over the decades, leading to inefficiencies, delays in the adoption of technology and a number of missed opportunities.

The advent of genomic selection has led to the re-emergence of quantitative genetics as a framework for incorporating marker and sequence information to supplement and complement standard phenotype descriptors and pedigree information. Technological changes are now bringing together the biometrical approach of animal breeders and the Mendelian approach of plant breeders. The deployment of modern sequencing methods to identify large numbers of molecular markers, and the emergence of cost-effective high

throughput genotyping and phenotyping technologies for crops and animals is not only revolutionizing breeding but offering new incentives for the migration of information and approaches between plant and animal breeding and for the unification of breeding efforts and biological discovery efforts.

Genomic selection a unifying theme across species

In 2001 a landmark paper¹⁸, which followed earlier work, notably by Lande and Thompson (1990)¹⁹ Nejati-Javaremi *et al.* (1997)²⁰, ²¹Lynch and Walsh (1998)²², Bernardo (1998)²³, Haley and Vischer (1998)²⁴ (who coined the term ‘genomic selection’), and, Whittaker *et al.* (2000)²¹, anticipated the availability of affordable high-density genomic data and proposed statistical methods that enabled this type of data to be used to increase the accuracy of selection. This method came to be called genomic selection. Subsequent modeling showed that genomic selection could have a large impact on genetic progress²⁵ and the technology was quickly adopted across a range of livestock species. Depending on the biology and economics of particular species and the breeding and production systems in which they reside, genomic selection has had different roles to play. In dairy cattle breeding in advanced economies, genomic selection has largely replaced progeny testing, enabling the generation interval to be shortened from five years to two years with consequent increases in rates of genetic gain. For example, in the Netherlands on-farm production levels increased by 21 index points per year in the seven years prior to the adoption of genomic selection in 2008. Since the adoption of genomic selection, on-farm production levels increased by 34 index points per year, a 60% increase. The generation interval of sires of sires, the key pathway through which genetic gain is achieved in dairy cattle breeding programs, has reduced from ~2,500 days to ~1,250 days²⁶. In pig breeding for commercial production systems, genomic selection has resulted in increased accuracy of selection and a better alignment of selection accuracy with the breeding goal, which has driven a 35% increase in rate of genetic gain in the breeding program that supplies the genetics in 25% of the commercially raised pigs globally (W. Herring, personal communication). In other species, such as extensive beef and sheep, genomic selection has provided the technology leap required to enable scientific breeding programs to be much more effective.

While genomic selection was adopted rapidly across the advanced livestock sectors and at a somewhat slower pace in international seed houses, the uptake has lagged in public sector plant breeding programs and developing world plant and animal breeding programs. Major international seed companies are routinely using genomic selection and many public sector breeding programs are exploring the technology or partially utilizing it, particularly for clonally propagated long-lived perennials²⁷. The explanations for this lag are complex and include the difference between the skills of a typical field-based plant breeder and the skills required to implement genomic selection, the barrier to entry created by the expense of investing in the computational and recording infrastructure and the genotype and phenotypic data required to effectively implement genomic selection, the complexity of the

genomes of many plant species, and the fact that plant and animal breeding have diverged somewhat over the decades and that it takes some time for advances in one field to be translated to the other. On the other hand, some argue that plant breeders can derive some of the expected benefits of genomic selection through other technologies and methods. For example, the application of doubled haploid technology²⁸ can reduce generation time significantly and plant breeders can get more reproducible estimates of phenotype by replicating clones and inbreds across generations and sites.

Effective implementation of genomic selection is expensive and requires specialist skills, creating large barriers to entry. However, because many of the skills and resources are broadly applicable, interdisciplinary and collaborative networks that bring together breeding programs for different plant species as well as animal species could enable widespread adoption of genomic selection across the many small-scale breeding programs in the developing world. This is because, despite the differences between species (within and between plant and animal kingdoms) in terms of their genomes, breeding mechanisms, etc., they require similar concepts and tools to enable genomic prediction. Thus, plant and animal breeding will benefit from working together to address questions that are common to the two disciplines, e.g. prediction in structured populations⁵. The cross-fertilization of ideas will develop a critical mass around which more can be done per unit of resource, and help to produce a new cadre of better skilled scientists.

Additionally, the skills and resources that would be assembled for genomic selection could serve as powerful platforms for biological discovery and for enabling the dissection of the true relationship between genomes and traits, and increasing the frequency of favorable alleles in breeding programs. For example, the major pig, poultry and cattle breeding programs have assembled data sets with several hundreds of thousands or even millions of individuals with dense genomic and phenotypic information, and results in the public domain suggest that international plant breeding organizations have done the same, at least for maize. Regarding developing world agriculture, while the Consortium of International Agricultural Research Centers (CGIAR) works on a number of plant and animal species, it could synergistically combine its resources and expertise (e.g. for pre-breeding, conventional and molecular breeding, and other research and translation activities) by centrally coordinating activities in genomic selection across its network. This will allow the exchange of knowledge and expertise between programs working on different species to develop deeper and more general insights than what is achievable in the individual programs. We believe that quantitative genetics provides an objective framework for doing this and that four different aspects need to be considered: (i) The breeder's equation; (ii) Unification of biotechnology and quantitative genetics; (iii) Integrating plant and animal breeding concepts and approaches; and (iv) Unification of breeding and biological research.

The breeder's equation – opportunities for more gain

The optimal design of any breeding program involves harnessing several scientific disciplines including genetics, statistics, computer science, physiology, molecular biology, logistics, economics, and social science. The breeder's equation, originally introduced by Lush¹⁵ provides a framework through which the impact of each of these disciplines, their underlying technologies, and choices about how they are used can be evaluated^{22,29}. The equation models the expected change in a trait in response to selection and can be written as $R = \frac{\delta_g \times i \times r}{L}$, where R is the change in trait mean per year, δ_g is the amount of genetic variation within the population; i is the selection intensity, r is the accuracy of the selection, and L is the generation interval.

Genomic selection directly addresses the four factors that affect the rate of genetic gain in animal and plant breeding³⁰:

- (i) Breeding is faster because breeders can recycle individuals more quickly if selection is based on genomic estimated breeding value (GEBV), which is generally more effective than that based on phenotype.
- (ii) Selection intensity is greater because breeders can select more individuals genotypically than phenotypically: genotyping cost is typically lower than phenotyping cost so more candidates for selection can be evaluated. This is particularly important in plant breeding.
- (iii) GEBV can be more accurate than estimated breeding value based on phenotype and pedigree alone.
- (iv) Genomic selection tools can also make integration of novel genetic material much more efficient³¹ through application of i-iii above in wide-crosses and pre-breeding programs, and through the use of optimal contribution theory driven by genomic information.

Unification of biotechnology and quantitative genetics

The application of biotechnology has had a profound effect on plant and animal breeding; in some cases this has been at the expense of quantitative genetics and selection theory⁵. Genomic selection offers an opportunity to build common grounds between biotechnology and quantitative genetics. Quantitative genetics is the study of the genetics of complex traits that are controlled by a large number of loci and often involve non-genetic factors³². Sequencing and resequencing of crop and animal genomes provide the opportunity to identify genome-wide genomic polymorphisms and correlative relationships between mutations and complex traits. However, causative mutations are more difficult to decipher, particularly in regions of high linkage disequilibrium³³. The potential of CRISPR/Cas 9 for genome editing in theory will provide new ways of validating causative effects particularly for traits that exhibit complex modes of inheritance³⁴. Furthermore, simulation studies³⁵ have recently shown how genome editing technology can be coupled

with genomic selection and double the rate of genetic gain compared with genomic selection conducted in isolation. This novel approach for deploying genome editing in breeding programs, referred to as PAGE (promotion of alleles by genome editing), has considerable potential to accelerate genetic gain in plant and animal improvement programs. In animal breeding, the cost of genotyping and resequencing has reached a point where producers and multipliers, in addition to members of the breeding nucleus (Figure 2), can be genotyped and have sequencing information accurately imputed for a modest investment. The population of genotyped or sequenced animals is therefore of the order of millions (e.g., in Ireland more than one million beef cattle are being genotyped; in major pig and poultry breeding programs similar data sets have been genotyped and are being imputed to whole genome sequence data) and for these, on-farm or slaughterhouse phenotype data are also available. Moreover, in addition, this huge resource can be treated as a genome-wide association mapping panel, which can be used as part of a cascade of technologies³⁶, to detect causative variants of quite small effect with great power, which can then be used as targets for genome editing. Only small numbers of editing events are required to make substantial improvement in genetic gain. In plant breeding, the number of genetically different individuals in production is much smaller (Figure 2), so a directly comparable approach to PAGE in animals may not be so applicable. However, in many minor and so called ‘orphan’ crops with less advanced breeding programs, cultivars released for production can be quite genetically diverse. If relevant phenotypic data can be collected on individuals, then there may be an opportunity to introduce these methods more rapidly in these cases. This might apply, for example, to some tree species.

Integrating plant and animal breeding approaches

The various plant and animal species used in agriculture have different biological systems and are farmed in different environments or within different economic settings. Thus, they require breeding programs that are specifically tailored. However, the underlying principles of breeding programs are common, and generic approaches could be devised for local deployment and adaptation. Recently, Gaynor *et al.*³⁷ proposed the reorganizing of traditional plant breeding programs for inbred or hybrid crops into two distinct parts as a strategy for implementing genomic selection (Figure 3). The first part is a population improvement part that develops improved germplasm. The second part is a product development component that identifies new inbred varieties or parents for hybrids. The first part is highly analogous to a classical animal breeding program based on recurrent selection and could make use of all of the tools and techniques that are well established in that domain. These include optimal contribution theory, economic selection indices, short generation intervals, multiple trait evaluation and selection- techniques that are not widely used in plant breeding. The second part is highly analogous to a classical plant breeding program and could similarly make use of all the tools and techniques that are well established in that domain, supplemented by careful use of genomic selection. Stochastic

simulations showed that the program using the two-part strategy generated more than 2.5 times the rate of genetic gain of the conventional program and nearly 1.5 times the genetic gain of the best performing program using an alternative genomic selection strategy based on a standard plant breeding program design for the same cost and in the same amount of time (Figure 3). The results also illustrate the synergy that can be realized by integrating plant and animal breeding approaches under the umbrella of a common platform.

Figure 3

In plant breeding there has been a proliferation of powerful high-throughput phenotyping technologies in recent years which are enabling more accurate characterization of traits and environments along time series³⁸. The expertise in the analysis and utilization of these data, as well as the long-established expertise in the integration of physiological models and quantitative genetics models³⁹, are examples, of which there are many, of the types of thinking, tools, and technology that are common in plant breeding that could be translated into animal breeding.

Unification of breeding and biological research

Access to large scale sequence and phenotype information at unprecedented scales will also provide opportunities to unify discovery biology and breeding. In other words, breeding programs will become ‘test beds’ for hypotheses as well as platforms for development and deployment of new varieties and breeds of livestock and fish that deliver multiple benefits. The largest impact of such developments will be in the areas of quantitative or complex traits that have been less amenable to reductionist approaches (as breeders now have ways of predicting the effects of causative factors through genomic selection) and are likely to deliver major benefits for crop and animal improvement programs. In this way, genomic selection may catalyze a unification of breeding methods, tools, and technologies across several plant and animal species, which in turn can advance the modernization of other aspects of breeding programs. These could include the widespread adoption of clearly defined breeding goals, economic selection indices, objective quantification of genetic gains, modeling, new trial design and analysis, and the efficient optimization of resources that underpin both breeding and biological discovery research.

Conclusions

The greatest and most immediate opportunity for the application of genomic selection is in the developing world where the demands and needs are greatest⁴⁰. The recently launched Excellence in Breeding Platform of the CGIAR (see URLs) is designed to create economies of scale, unify breeding ideas, technology, resources and demand and capacity across species and systems to modernize breeding programs that are focused on meeting the needs of small holder farmers in the developing world. This approach is summarized in Figure 4 and embraces many of the concepts outlined in this article and is designed to deliver innovative

‘step changes’ in the rate of genetic gain for crops, livestock and fish of relevance to the developing world.

Figure 4

The successful implementation of genomic selection for the delivery of public goods for the developed and developing world will require a strategic approach to the design of breeding programs, greater collaboration, new partnerships that span the public and private sector, and new skills. However, the impact of genomic selection may extend beyond the creation of new varieties and improved livestock to include an integrative framework for simultaneous delivery of both scientific discoveries and new products for the developing world. This may represent the biggest incentive for enhanced and global coordination of funding to support modern plant and animal breeding programs.

URLs-

<http://excellenceinbreeding.org>

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Author Contributions-

T.C., I.M., J.H. and W.P. jointly developed the ideas and wrote the paper.

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Figure Legends-

Figure 1 Some key milestones of selective animal and plant breeding

Figure 2 Comparison of animal and plant breeding approaches. In some areas plant and animal breeders have adopted similar approaches. All breeding programs can be thought of as having two basic components: (i) a recurrent selection component that seeks to increase the frequency of favorable alleles in a population that in turn increases the mean of the population; and (ii) a product development component that seeks to extract genotypes from this improved population for a farmer to grow. A major difference between animal and plant breeding has been that the former places greater emphasis on population improvement with product development consisting primarily of multiplication of stock which is not recycled into the breeding nucleus, whereas in the latter greater emphasis is placed on selection of an improved product, in the form of a recognizable plant variety, which is often also the source of parents for the next breeding cycle. That is, while varieties (often protected by plant breeders' rights) are the focus in plant breeding, the concept is almost irrelevant in animals.

Figure 3 A variant of the two-part breeding program design for plant breeding

Figure 4 Capturing new opportunities to accelerate the pace of genetic gain based on efficient and targeted access to genetic diversity, coordinated phenotyping across environments, cost effective sequencing, genomic prediction and genome editing

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Animals

Domestication ~12000 years ago

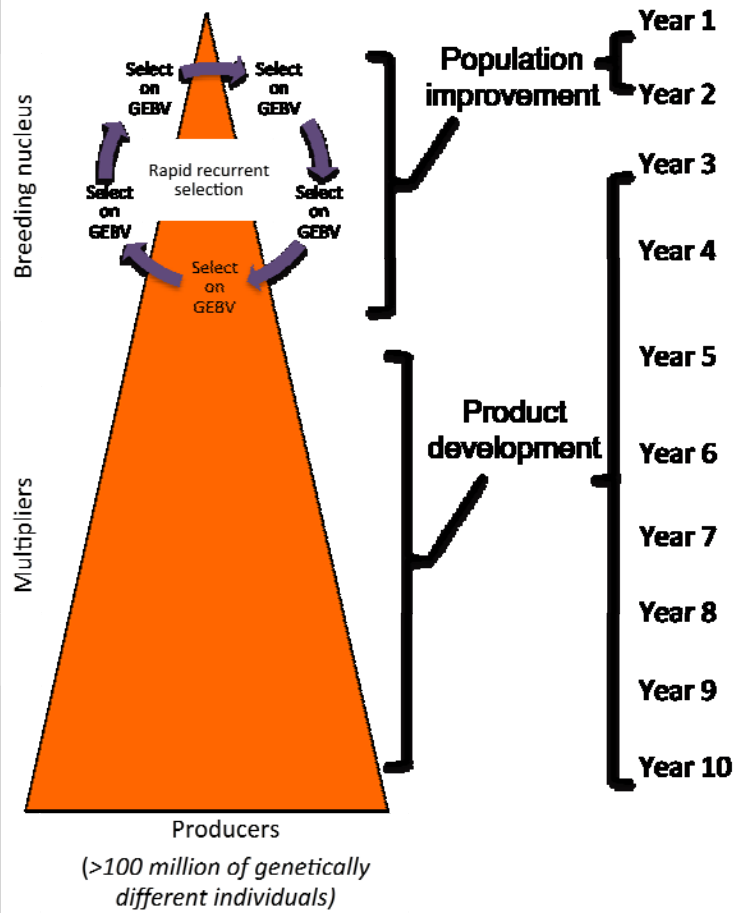
- 1886** Concept of regression to describe relationship between offspring and parents (Galton)
- 1908** Law of population genetics (Hardy; Weinberg)
- 1918** Population genetics introduced as an extension of the laws of inheritance (Fisher, Wright, Haldane)
- 1935** Improved breeding methods (Lush)
- 1950** Estimation of breeding values as random effects (Henderson)
- 1953** Model for DNA structure (Watson & Crick)
- 1960** Quantitative genetics (Falconer)
- 1972** Genetic engineering, first recombinant DNA molecules (Berg)
- 1975** Best linear unbiased prediction (BLUP) (Henderson)
- 1980s** Biotechnology, from the early 1980s
- 1990** Molecular markers used for improved selection (Lande and Thompson)
- 2001** Introduction and application of genomic selection (Meuwissen et al)
- 2013** CRISPR/Cas9 based genome editing

Plants

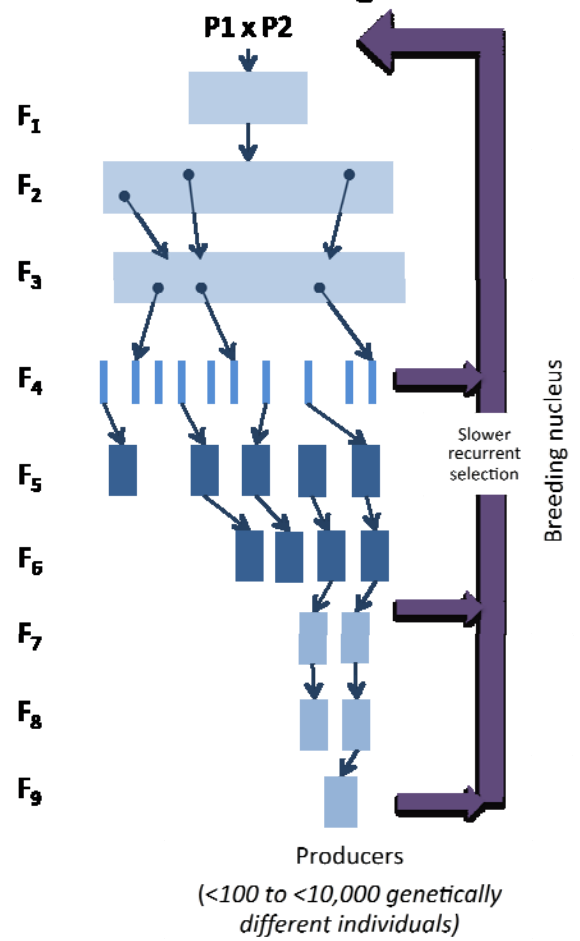
Domestication ~ 12000 years ago

- 1860s** Discovery of the rules of inheritance (Mendel)
- 1903** Pure-line breeding theory (Johannsen)
- 1908** Hardy-Weinberg law
- 1908** Exploitation of heterosis (Shull)
- 1910** Modern pedigree selection (Nilsson-Ehle)
- 1920** Mutation breeding (Stadler)
- 1939** Concept of single seed descent breeding method (Goulden)
- 1945** Recurrent selection method of breeding (Hull)
- 1952** Methods for double haploid lines (Chase)
- 1953** Model for DNA structure (Watson & Crick)
- 1970** Nobel Prize for the Green Revolution (Borlaug)
- 1980s** Biotechnology, from the early 1980s
- 1983** Nobel Prize for discovery of mobile genetic elements (McClintock)
- 1990** Molecular markers used for improved selection (Lande and Thompson)
- 1994** First approval of commercial GM variety
- 1998** Best linear unbiased prediction based on trait and marker data (TM-BLUP), a form of genomic selection, introduced (Bernardo)
- 2001** Introduction of theoretical approaches to genomic selection (Meuwissen et al)
- 2010s** Application of genomic prediction in plant breeding
- 2013** CRISPR/Cas9 based genome editing

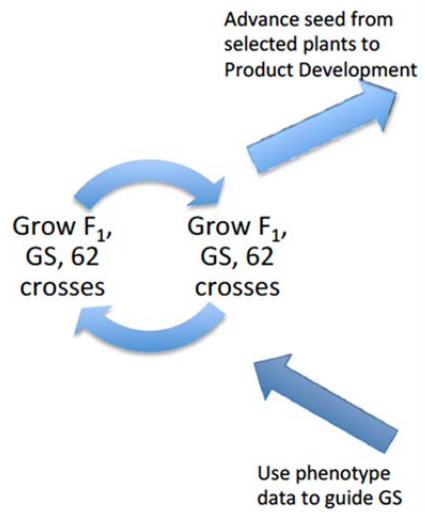
Animal breeding



Plant breeding



Population Improvement



Product Development

Year	Generation		Number of Plants	Action
1	F_1		124 half-sib families	Increase in greenhouse
2	F_2		1000 plants per family	Bulk 50 plants per family
3	F_3		1000 plants per family	Bulk 50 plants per family
4	F_4		1000 plants per family	Derive new lines from 50 plants per family
5	$F_{4:5}$		6200 headrows	Advance 1000 lines
6	PYT, $F_{4:6}$		1000 lines	Yield trial, genotype
7	AYT, $F_{4:7}$		100 lines	Yield trial
8	EYT, $F_{4:8}$		10 lines	Yield trial
9	EYT, $F_{4:9}$		10 lines	Yield trial
10	$F_{4:10}$		1 line	Release variety

